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INTERSPECIFIC AGGRESSION BETWEEN *FORMICA RUFA* L.
AND *FORMICA CUNICULARIA* LATR. (**)

(Hymenoptera Formicidae)

Abstract. — Aggression between members of *Formica rufa* and *Formica cunicularia* ant-workers was followed both in the laboratory and in the field. The aggressive behaviour of the former species was quantified by frequencies of threat, gaster flexing, seizing, dragging, and carrying. Conflict measures such as mutual investigation, latency to attack and accumulated attacking time, were also recorded in seconds. In the field, the incidence of fightings was higher than in laboratory paired ants, being intruders of both species always immediately seized and dragged by several resident workers of the opposite colony in a fierce and prolonged co-operative attack. A certain amount of mutual investigation was recorded in laboratory pairs, where attack behaviour was not always performed and no one ant was killed in the experimental time. With regard to *F. cunicularia*, *F. rufa* interspecific aggression was lower than that recorded in the related wood-ant species *F. lugubris* in the same experimental situations.

Riassunto. — *Aggressione interspecifica tra Formica rufa L. e Formica cunicularia Latr.* (Hymenoptera Formicidae).

E' stata analizzata, sia in laboratorio che in natura, l'aggressione tra membri di *Formica rufa* e *Formica cunicularia*. Si è soprattutto quantificato il comportamento aggressivo della prima specie, considerando le frequenze relative alla minaccia, flessione dell'addome, presa, trascinamento e trasporto. Sono state anche registrate, in secondi, le misure del conflitto quali l'investigazione reciproca, la latenza all'attacco e il tempo totale speso nella lotta. In natura, l'incidenza del combattimento è stata più elevata rispetto a quella osservata nelle coppie eterospecifiche di formiche sperimentate in laboratorio. Infatti, gli intrusi di entrambe le specie venivano sempre afferrati all'istante e trascinati da diverse operaie residenti dell'opposta colonia, in un violento e prolungato attacco cooperativo. In laboratorio è stato invece registrato un certo grado di mutua investigazione: non tutte le coppie considerate hanno com-

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battuto e, comunque, nessuna formica è rimasta uccisa nel tempo sperimentale. Dai risultati ottenuti è possibile affermare che l'aggressione interspecifica di *F. rufa* nei riguardi di *F. cunicularia* rimane certamente a livelli più bassi di quella espressa dalla specie affine *Formica lugubris* nelle stesse situazioni sperimentali.

Introduction.

Both within and between species reciprocal conflict has been frequently observed in neighbouring colonies of ants (for reviews see: WALLIS, 1964; BRIAN, 1965; WILSON, 1971; CARROLL & JANZEN, 1973; HÖLLDOBLER, 1976, 1979; DUMPERT, 1981).

These territorial fightings may be regarded as aspect of predatory behaviour or as expression of sympatric nest competition for food sources, though in many cases it is difficult to determine whether a spacing rather than a predatory response is involved (cf. DOBRZANSKA & DOBRZANSKI, 1962; WALLIS, 1962 b; DOBRZANSKI & DOBRZANSKA, 1975; CZECHOWSKI, 1976, 1977, 1979; BRIAN, 1978; BARONI URBANI, 1979; DE VROEY, 1979 a, b; HÖLLDOBLER & LUMSDEN, 1980).

For example, the existence of territory and fighting (in which predatory behaviour seems to be involved) between nests in some red wood-ants belonging to *Formica rufa*-group (BETREM, 1960) has been recorded many times (cf. HOLT, 1955; ZACHAROV, 1969; DE BRUYN, 1972, 1978; DE BRUYN & MABELIS, 1972; REZNIKOVA, 1974; BREEN, 1976; MABELIS, 1979 a, b; CHERIX & GRIS, 1978).

In particular, *F. rufa* inter-nest hostility is performed by spring battles, which suggest social establishment and following maintenance of territory in the early season (cf. ELTON, 1932; MARIKOVSKY, 1962; BRIAN, 1965; DE BRUYN & KRUK-DE BRUYN, 1972; SKINNER, 1980).

In order to distinguish inter- and intra-specific forms of aggression in *Formica rufa*-group species, we have recently analysed these behaviours in *Formica lugubris* Zett. (LE MOLI & PARMIGIANI, 1981, 1982; LE MOLI et al., 1981), a very useful predatory species used as biocontrol agent in forests (PAVAN, 1960).

Moreover, studying *Formica rufa* L. intercolonial relationships, we found that this species is less aggressive than *F. lugubris*, as far as intraspecific interactions are concerned (LE MOLI et al., 1982).

To make comparison between these closely related species of wood-ants, in this present work we attempted to study interspecific combat in *F. rufa*, being *Formica cunicularia* Latr. the opponent species, as previously done in *F. lugubris* interspecific conflict analysis.

Materials and methods.

The experiments were carried out both in field and in laboratory situations, as described in LE MOLI & PARMIGIANI (1981).

The nests considered were located in the Apennines of the Lombardy Region (Italy), at about 1100 m high, being *F. rufa* ant-hill (= FR) at Casa Piazza locality and *F. cunicularia* nest (= FC) on the Mount Penice in a place remote from the former. Ants and nest materials of the two species were collected and housed in the laboratory in artificial nests under controlled conditions: relative humidity was at 60-80% and room temperature about 18-21 °C.

In the laboratory, pair test was performed introducing two ants (*F. rufa* = fr, and *F. cunicularia* = fc), matched for size, to the fighting box (9 × 9 × 3 cm). Test duration was of 15 minutes. The same items of behaviour (i.e. mutual investigation = MI, latency to attack = LA, accumulated attacking time = AAT) were measured in seconds using our previously described techniques (LE MOLI & PARMIGIANI, 1981).

We also recorded the frequencies of the following elements of conflict behaviour (see also WALLIS, 1962 a; DE VROEY, 1980): threat with open mandibles, gaster flexing, seizing, dragging, and carrying.

As controls, pairs of ants belonging to the same colony, namely fr vs fr and fc vs fc, were tested in the same situation.

Field test was carried out with previously described techniques (LE MOLI & PARMIGIANI, 1981). In fact, after a week of laboratory housing, ant-workers of *F. cunicularia* (fc), used as intruders, were individually introduced in the vicinity of the *F. rufa* ant-hill (FR), and vice-versa. The response of resident ants was observed for two minutes recording the same elements of behaviour displayed by ants in laboratory conditions. As controls, individuals of *F. cunicularia* and *F. rufa* were re-introduced to their original colony and nest-mates behaviour was observed for an identical period of time.

Results.

Laboratory pair test.

Data for this test are presented in Table 1.

No signs of aggression were observed in the controls, which displayed only « startle responses » (50% in fr vs fr, and 75% in fc vs fc encounters) at the first contact, showing an equal time of MI.

If one considers the outcome of the interspecific interactions (fr vs fc), it is evident that ants attacked each other (see LA and AAT values),

even though attack behaviour was not always performed (see proportion of fighting pairs). Moreover, in several cases the two ants had a certain amount of mutual inspections (see MI value) before attacking and/or during a pause in the attack. However, no one ant was killed in the experimental time, whereas 4 *F. cunicularia* were found death after 1 hour. In this connection, it must be remembered that *F. rufa* is normally bigger than *F. cunicularia* and possesses formic acid that may be also squirted as offensive weapon.

TABLE 1. — Median measures (with ranges) of conflict behaviour between *Formica rufa* (fr) and *Formica cunicularia* (fc) paired in 15 minute laboratory tests (a); *b* and *c* are controls.

Encounter	Pairs tested	Proportion of fighting pairs	MI (secs)	LA (secs)	AAT (secs)	No. of attacks
a) fr vs fc	18	12/18	4.25 (0-135)	32.5 (1-900)	33.6 (0-860)	1 (0-6)
b) fr vs fr	16	0/16	85.3 (15.3-197.2)	+900 (900-900)	0 (0-0)	0 (0-0)
c) fc vs fc	16	0/16	114.0 (19-730)	+900 (900-900)	0 (0-0)	0 (0-0)

MI values: *a* differs from *b* and *c*, $p < 0.002$ (Mann-Whitney 'U' Test).
b does not differ from *c*.

LA values: *a* differs from *b* and *c*, $p < 0.002$ (Mann-Whitney 'U' Test).

AAT values: *a* differs from *b* and *c*, $p < 0.002$ (Mann-Whitney 'U' Test).

N° of attacks values: *a* differs from *b* and *c*, $p < 0.002$ (Mann-Whitney 'U' Test).

Both ants used the mandibles attacking each other, and the parts of the body seized more frequently were the legs, petiolar connection, and antennae which were sometimes cutted.

Concerning the elements of behaviour performed by *F. rufa* during the conflict, they included: threat (50%), seizing (33.3%), and dragging (22.2%), but the most frequent behaviour was the gaster flexing (accompanied by squirting of formic acid), appearing in 72.2% of the contests. No carrying was observed.

Field observations.

Data are presented in Table 2. The results are in agreement with those obtained in laboratory test.

When ant-workers were individually re-introduced in their own colony (fr vs FR, fc vs FC) after a week of separation, they were recognized in a short while by antennal inspections, and soon accepted by nest-mates. Such phenomenon, which was more rapid in *F. cunicularia* (see MI

TABLE 2. — Median aggressive measures (with ranges) towards a heterospecific intruder (fc, fr) by resident members of *F. rufa* (FR) and *F. cunicularia* (FC) colonies in field observations (*a*, *b*); *c* and *d* are controls (12 replications in each trial).

Trial	Proportion of intruders attacked	MI (secs)	LA (secs)	AAT (secs)
<i>a</i>) fc vs FR	12/12	0 (0-0)	1 (1-4)	100 (26-115)
<i>b</i>) fr vs FC	12/12	0 (0-0)	1 (1-11)	119 (105-119)
<i>c</i>) fr vs FR	0/12	7 (2-23)	+120 (120-120)	0 (0-0)
<i>d</i>) fc vs FC	0/12	0 (0-4)	+120 (120-120)	0 (0-0)

MI values: *c* differs from categories *a* and *b* (highly significant); and from *d*, $p < 0.002$ (Mann-Whitney 'U' Test).

LA values: *a* and *b* differ from categories *c* and *d* (highly significant) (Mann-Whitney 'U' Test).
a does not differ from *b*.

AAT values: *a* and *b* differ from categories *c* and *d* (highly significant);
a differs from *b*, $p < 0.002$ (Mann-Whitney 'U' Test).

values), suggests that in both species colony's odour does not appear to have been lost during the week of laboratory housing.

Concerning the interspecific relationships (fc vs FR, fr vs FC), the intruders were immediately attacked by several resident workers when placed in the vicinity of nests. Therefore, the two species share the same

behaviour towards heterospecific aliens (see MI and LA values), which were involved in a prolonged combat, longer in *fr vs FC* contest (see extended AAT). In fact, the engaged conflict summoned other ants which assisted conspecific in attacking the intruder. This « catalitic » effect was particularly evident in *F. cunicularia*. In fact, also the re-introduced individuals, housed in laboratory for a week and recognizable by a white spot painted on the abdomen, cooperated with conspecifics during the nest defence.

In *fc vs FR* contest, the elements of conflict behaviour displayed by *F. rufa*, especially threat, gaster flexing and seizing (100% in all cases), were much more obvious in the field in spite of the minor recording time (cf. laboratory test), probably because of the animal's familiarity with its surroundings. The parts of the body frequently seized were antennae, legs and petiole. In 50% of the cases intruders were dragged towards the nests, whereas carrying was not observed.

Seizing (100%) and dragging (41.6%) were also performed by *F. cunicularia* residents on *F. rufa* intruders, being antennae and legs the parts of the body seized. It is very interesting to note that even if *F. cunicularia* does not possess formic acid, in 25% of the cases gaster flexing was observed.

Conclusions and discussion.

This study points out that the two species considered show marked interspecific aggression. This behaviour was particularly evident in field observations, probably because of a territorial effect as claimed in several species of ants (cf. WILSON, 1971; CARROLL & JANZEN, 1973; HÖLLDOBLER, 1976, 1979; BARONI URBANI, 1979; MABELIS, 1979 b).

In fact, whereas in the natural context the contact was immediately followed by a fierce attack, in the laboratory sometimes paired ants displayed a certain amount of MI limiting, in this case, their performances of overt aggression to threat and/or gaster flexing. Really no killing was observed during laboratory experimental time.

The main difference observed in the patterns of attack employed by the two species against heterospecific intruders concerns the gaster flexing, which was always performed by *F. rufa* and only seldom by *F. cunicularia*. It is worth noting that gaster flexing was accompanied by squirting of formic acid, which is a common substance used as a weapon in *F. rufa*-group. Formic acid acts also as alarm pheromone (cf. MASCHWITZ, 1964; WILSON, 1965; BUTLER, 1967; LÖFQVIST, 1976), stimulating the nearby conspecifics to attack the alien as seen in this case in natural situation. Nevertheless the catalitic effect of an engaged fight was also well evident

in *F. cunicularia*, so that even the re-introduced nest-mates cooperated with conspecifics in nest defence.

Dragging behaviour performed by *F. rufa* on the intruder, which usually layed motionless, was always directed towards the nest. Since *F. rufa* is a predatory species, it is likely that this pattern may be regarded as an aspect of predatory behaviour.

Considering aggressiveness in *F. rufa* it is possible, on the basis of the elements of behaviour, to distinguish between intra- and inter-specific form aggression, being the former characterized by threat and « upright posture » (cf. LE MOLI et al., 1982) whereas the latter is accompanied by gaster flexing and/or overt attack.

Taking into account the previous results on conflict behaviour between *Formica lugubris* and *F. cunicularia* (cf. LE MOLI & PARMIGIANI, 1981), it must be considered that *F. rufa* is less aggressive than the closely related species *F. lugubris*. One thing is also certain: the aggressive attitude of one species, at least in laboratory conditions, modulates the opponent behaviour (cf. the behaviour displayed by *F. cunicularia* against *F. lugubris* in the same experimental situations).

Concerning our results on these subjects (LE MOLI & PARMIGIANI, 1981, 1982; LE MOLI et al., 1981, 1982), it is possible to conclude that *F. rufa* is less aggressive than *F. lugubris* either with regard to intra- or inter-specific aggression. It may therefore be argued that a continuity exists between these two forms of aggression.

Further experiments are scheduled to analyse the aggressive interactions between *Formica lugubris* and *Formica rufa*, since they could be useful as a taxonomic tool in the *Formica rufa*-group.

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